State of California THE RESOURCES AGENCY Department of Fish and Game

POPULATION ECOLOGY OF THE NORTHERN SPOTTED OWL (Strix occidentalis caurina)
IN NORTHWEST CALIFORNIA: PRELIMINARY RESULTS, 1988¹

b y

Alan B. Franklin, Jennifer A. Blakesley and Ralph J. Gutierrez

Department of Wildlife

Humboldt State University

Arcata. CA 95521

March 1989

ABSTRACT

In 1988, we surveyed 88 Northern Spotted Owl territories in northwest California, 43 on the 292 km² Willow Creek Study Area (WCSA) and 45 on the 10,000 km² Regional Study Area (RSA). Of the 123 owls located and identified to age, 10.6% were subadults. We found 72 Spotted Owls on 37 occupied territories in the WCSA. Reproductive parameters in northwest California remained stable from 1985 through 1988 with 67.8% of the pairs nesting and 41.2% fledging young. Mean number of young fledged per pair was 0.65 with adult females fledging significantly more young than In 1988, female turnover rates (26.0%) were significantly greater than male turnover rates (9.3%). a nine-fold increase in inter-territorial movements by banded adults and subadults on the WCSA compared to the previous three These movements contributed to the abandonment of four territories but also to the formation of four new territories. Documented dispersals of banded juveniles in the WCSA declined to zero in 1988. Annual survival estimates were calculated for juveniles (0.06), subadults (0.77) and adult males (0.96) and adult females (0.87) using empirical methods. Adult survival rates estimated using the Jolly-Seber mark-recapture model were similar to rates estimated using empirical methods.

Supported by California Environmental License Plate Fund and 1987 Special Legislative Spotted Owl Allocation, Nongame Bird and Mammal Section, Wildlife Management Division, Job II.A.2, and USDA Forest Service, Pacific Southwest Forest and Range Experiment Station Research Cooperative Agreement PSW-87-0011CA. Progress Report.

FINAL REPORT TO

CALIFORNIA DEPARTMENT OF FISH AND GAME CONTRACT FG7502 (FY 1987-88)

AND

USDA FOREST SERVICE
PACIFIC SOUTHWEST FOREST &, RANGE EXPERIMENT STATION
RESEARCH COOPERATIVE AGREEMENT PSW-87-0011CA (FY 1987-88)

Submitted February 1989

POPULATION ECOLOGY OF THE NORTHERN SPOTTED OWL (Strix occidentalis caurina) IN NORTHWEST CALIFORNIA: PRELIMINARY RESULTS, 1988

CONTRACTOR
Humboldt State University
Arcata, CA 95521

PROJECT LEADER
Alan Franklin
Department of Wildlife
Humboldt State University
Arcata, CA 95521

RESEARCH ASSOCIATE
Jennifer A. Blakesley
Humboldt State University Foundation
Humboldt State University
Arcata, CA 95521

PRINCIPAL INVESTIGATOR
Dr. R. J. Gutiérrez
Department of Wildlife
Humboldt State University
Arcata, CA 95521

RESEARCH ASSISTANTS Christine Moen, Kendal Young and Marc Kasper

TABLE OF CONTENTS

	Page
LIST OF TABLES	i i
LIST OF FIGURES	iii
LIST OF APPENDICES	iii
INTRODUCTION	1
STUDY AREA	1
TERMINOLOGY	4
METHODS Surveys Capture Determining Sex and Age Data Analysis	6 6 7 7 7
RESULTS Surveys Sex and Age-class Distribution Abundance and Density on the Willow Creek Study Area Reproduction Proportion of Population Nesting and Fledging Young Reproductive Output Site and Mate Fidelity Occupancy of Territories Movements Between Territories Annual Survival Juveniles Subadults Adults Effects of Fires	9 9 10 12 12 14 16 17 18 20 22 22 22 23
DISCUSSION	25
ACKNOWLDEDGEMENTS	26
LITERATURE CITED	27

LIST OF TABLES

Table	1.	Number of Northern Spotted Owl territories surveyed, occupied and checked for reproduction in 1988 on the Willow Creek Study Area (WCSA) and Regional Study Area (RSA), northwest California
Table	2.	Sex-specific distribution of adult and subadult Northern Spotted Owls located and identified to age- class in 1988 on the Willow Creek Study Area (WCSA) and Regional Study Area (RSA), northwest California10
Table	3.	Effort expended in surveying the Willow Creek Study Area, northwest California, from 1985 through 198811
Table	4.	Proportion of Northern Spotted Owl pairs checked for reproductive activity before 31 May which nested in the Willow Creek Study Area (WCSA) and Regional Study Area (RSA), northwest California, from 1985 through 198811
Table	5.	Proportion of nesting pairs of Northern Spotted Owls which fledged young in the Willow Creek Study Area (WCSA) and Regional Study Area (RSA), northwest California, from 1985 through 1988
Table	6.	Proportion of Northern Spotted Owl pairs checked for reproductive activity which fledged young in the Willow Creek Study Area (WCSA) and Regional Study Area (RSA), northwest California, from 1985 through 198813
Table	7.	Reproductive characteristics of paired subadult and adult female Northern Spotted Owls of known age on the Willow Creek Study Area and Regional Study Area, northwest California, from 1984 through 198814
Table	8.	Mean number of young fledged per pair of Northern Spotted Owls in the Willow Creek Study Area (WCSA) and Regional Study Area (RSA), northwest California, from 1985 through 1988
Table	9.	Mean productivity of Northern Spotted Owl pairs in the Willow Creek Study Area (WCSA) and Regional Study Area (RSA), northwest California, from 1985 through 1988
Table	10.	Annual turnover rates from 1984-85 through 1987-88 in territories occupied by banded male and female Northern Spotted Owls in northwest California

LIST OF TABLES (Continued)

Table 11.	Proportion of territories in the Willow Creek Study Area, northwest California, which were occupied by unpaired Northern Spotted Owls from 1985 through 1988
Table 12.	Number of Northern Spotted Owls identified in northwest California from 1984 through 1988 20
Table 13.	Empirical estimates of annual survival rates for juvenile, subadult and adult Northern Spotted Owls in northwest California from 1985 through 198822
	LIST OF FIGURES
Figure 1.	Map of Northern Spotted Owl territories (dots) surveyed in 1988 in the Regional Study Area, northwest California2
Figure 2.	Map of Northern Spotted Owls territories in the Willow Creek Study Area, northwest California, showing the location of occupied territories (dots) in 1988 3
Figure 3.	Age-class distributions of inter-territorial movements by banded Northern Spotted Owls for (A.) sex and (B.) year on the Willow Creek Study Area, northwest California, from 1985 through 1988
Figure 4.	Mean distances moved by banded juvenile, subadult and adult Northern Spotted Owls on the Willow Creek Study Area, northwest California, from 1985 through 198821
Figure' 5.	Mean survival estimates, with 95% confidence intervals, for adult male and female Northern Spotted Owls in northwest California from 1984 through 1988 24
	LIST OF APPENDICES
Appendix	1. Locations and occupancy of 43 Northern Spotted Owl territories in the Willow Creek Study Area, northwest California, from 1984 through 1988 31

INTRODUCTION

The Northern Spotted Owl (Strix occidentalis caurina) is closely associated with old-growth Douglas-fir (Pseudotsuga menziesii) forests in British Columbia, Washington, Oregon and northwestern California (Grinnell and Miller 1944; Gould 1974; Solis 1983; Forsman et al. 1984; Gutiérrez et al. 1984; Sisco 1984). Logging of these old-growth forests is considered to be a major factor in the decline of Spotted Owl populations (Gould 1977; U.S. Fish and Wildlife Service 1982; Forsman et al. 1984; Gould 1985). This decline is precipitating a growing controversy over the amount of old-growth forests necessary for the continued viability of Spotted Owl populations (Heinrichs 1984, Simberloff 1987).

The lack of basic demographic data has been a major problem in assessing the present and future status and management of Spotted Owl populations. In order to gain a better understanding of Spotted Owl demography, the California Department of Fish and Game initiated and funded the present five-year study in northwestern California. Redwood Sciences Laboratory of the USDA Forest Service provided funds in 1987 and 1988 to expand the sampling effort. The objectives of this study were to:

- 1) Assess reproduction of Spotted Owls in northwestern California from existing data as well as by monitoring a selected owl population;
- 2) Estimate the mate and territory fidelity of individual Spotted Owls;
- 3) Estimate annual survival rates; and
- 4) Estimate the rate of abandonment and re-occupation of territories known to have been active during the past four years.

This study was initiated in 1985. Results from the first, second and third years of study were reported in Franklin et al. (1986), Franklin et al. (1987), and Franklin and Gutiérrez (1988), respectively. In this report, we presented the results from the fourth year of the study, 1988. Information on density for the four-year period was reported elsewhere (Franklin et al., in press).

STUDY AREA

We studied Spotted Owls in two areas of northwest California (Figures 1 and 2). The regional study area (RSA) of approximately $10,000~\rm{km}^2$ (3,861 mi²) included portions of the Six Rivers, Klamath and Shasta-Trinity National Forests and lands

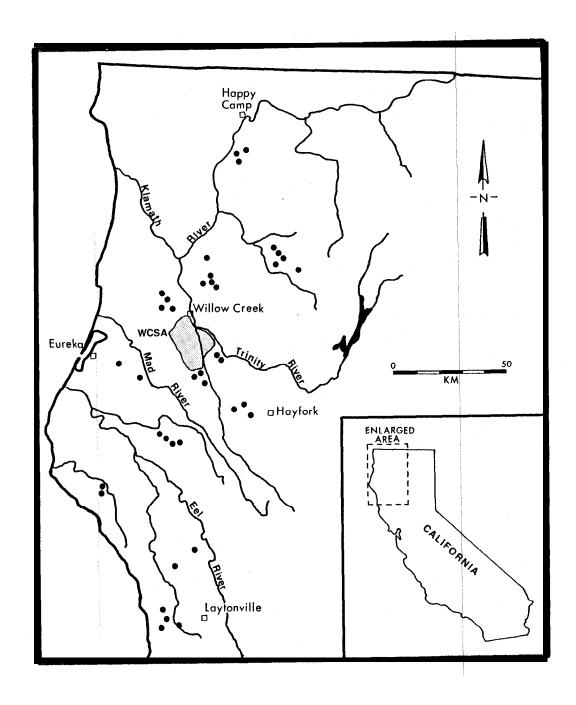


Figure 1. Map of Northern Spotted Owl territories (dots) surveyed in 1988 in the Regional Study Area, northwest California. Willow Creek Study Area (WCSA) shown as shaded area.

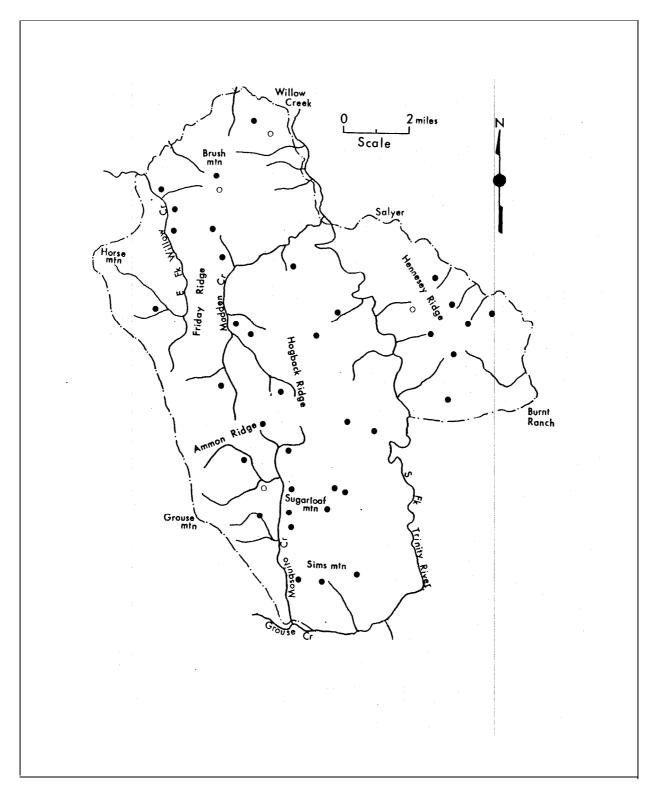


Figure 2. Map of Northern Spotted Owl territories in the Willow Creek Study Area, northwest California, showing locations of occupied territories (dots) in 1988. Open circles represent territories occupied in 1987 but abandoned in 1988.

administered by the U.S. Bureau of Land Management. The Willow Creek study area (WCSA) encompassed 292 km² (113 rni²) and was located just south of Willow Creek, Humboldt Co., California in the central portion of the RSA.

The WCSA was managed primarily by the Lower Trinity Ranger District, Six Rivers National Forest with a small portion managed by the Big Bar Ranger District, Shasta-Trinity National Forest. The dominant land use in the WCSA was timber production with clearcutting being the principal method of logging.

The WCSA was selected originally in 1985 for intensive study because (1) the study area was easily delineated by geographic boundaries, (2) the history of occupation by Spotted Owls was well known through previous surveys and research, and (3) the area was accessible by roads.

Climate within the study areas was characterized by cool, wet winters and hot, dry summers. Elevations ranged from 200 m (650 ft) to 1700 m (5580 ft). The vegetation was best described as Mixed Evergreen, Klamath Montane, Oregon Oak and Tan Oak forest types (Kuchler 1977). Additional description of the climate, physiography, and vegetation of the study area was presented by Franklin et al. (1986).

TERMINOLOGY

For this report, terms have been defined as follows:

<u>Juvenile</u> - a young owl that has left the nest (fledged) but has not acquired Basic I adult plumage (Forsman 1981).

<u>Subadult</u> - an owl that is at least one year old and less than three years old as determined by the shape and color of the tips of the owl's retrices (Forsman 1981).

Adult - an owl that is at least three years old as determined by the shape and color of the tips of the owl's retrices (Forsman 1981).

<u>Territory</u> - an area currently and/or historically used and actively defended by an owl or pair of owls. An owl was considered to be actively defending an area when vocal responses were elicited from the same bird in the same area on two or more occasions.

<u>Survey</u> - a systematic search of an area for Spotted Owls by observers using imitated calls to elicit responses from Spotted Owls. In a point survey, observers spend time (usually 10-15 min.) calling at the same location (a call station). In a cruise survey, observers, walk a route while calling. In walk-in

survey observers visually locate a calling owl at a daytime roost by following the owl's response. A nighttime survey consisted of one or more point and cruise surveys which covered part or all of a Spotted Owl territory.

Survey Effort - the amount of time devoted strictly to surveying for Spotted Owls by a two-person crew. Survey effort included time spent locating owls, determining reproductive status and identifying individuals by capture, recapture or re-sighting of color-bands. Time included in survey effort began when (1) the observer began using vocally imitated calls to detect a Spotted Owl or (2) the owl was detected before the observer began calling. Survey effort ended when (1) the observer stopped calling after not detecting an owl (e.g. during a point or cruise survey), (2) the observer or the owl(s) stopped calling (whichever occurred first) and no effort was made 'to determine reproduction or to identify individuals (e.g. during a point survey) or (3) when effort involved in determining reproduction and/or identity of individuals was completed (e.g. during a walkin survey). The definition for survey effort in Franklin et al. (1986, 1987) was based on effort expended by individuals (not crews) and did not include effort expended in attempting to identify individuals.

<u>Detection</u> - a positive location by either hearing a Spotted Owl response or by an actual sighting.

<u>Density</u> - the number of animals per unit area (Caughley 1977:12). Crude density was defined as the number of owls per total area while ecological density was the number of owls per unit of suitable habitat (Johnson 1978:11).

Productivity - number of fledged young per productive female (i.e. a female that has produced at least one young) per year. Postupalsky (1974) defined this term as the number of young per occupied nest. However, the number of nest attempts is difficult to assess for Spotted Owls because nest attempts may terminate within a short period of time. We defined productivity as the total number of young produced in a breeding population, which alone, is not solely a function of nest success and mean brood size (as defined by Postupalsky 1974).

<u>Turnover Rate</u> - the annual rate of change of individuals within a territory (Village 1985).

<u>Divorce</u> - a severing of the bond between mates even though both are alive and present as territorial individuals (Johnston and Ryder 1987).

<u>Survival Rates</u> - the probability of an individual surviving from one year to the next (Tanner 1978:70).

METHODS

We attempted to locate and identify all individual Spotted Owls in the WCSA and on selected territories in the RSA. Territories in the RSA were selected based on where Spotted Owls were banded during previous studies (Gutiérrez et al. 1985) and to provide a wider geographic sample for estimating demographic parameters. Spotted Owls were located using vocal imitations of their calls to elicite responses (Forsman 1983). Individuals were identified by initial capture, marking and subsequent recapture. Most of our methods were either adapted from Forsman (1983) or developed during previous research projects (Gutiérrez et al. 1984; Gutiérrez et al. 1985; Franklin et al. 1986). Methods for recording data collected in the field 'were described in Franklin et al. (1986).

Surveys

Both day and night surveys were used to locate Spotted Owls. Night surveys were conducted between dusk and 2400 hours (Pacific Standard Time) and consisted primarily of point surveys. A minimum of 10 minutes was devoted to any call station during point surveys.

Day surveys were used to locate roosting owls and consisted of walk-in surveys and cruise surveys. Walk-in surveys were initiated during the day at sites where owls had been located the previous night. Cruise surveys were conducted in habitat considered potentially occupied, but without any previous record of occupancy.

Sampling effort within the WCSA in 1988 included (1) call stations and survey routes established between 1985 and 1987 where owls responded (2) habitat considered to have a high probability of Spotted Owl use (habitat determination was based on habitat descriptions provided by Solis (1983), records of historical sightings, and personal experience) and (3) remaining habitat not considered suitable for Spotted Owls (Solis 1983). Survey effort, as defined in this report, was re-calculated for 1985 and 1986.

Once located, owls were checked for reproductive activity by feeding live mice to individuals (Forsman 1983). Breeding Spotted Owls take prey and fly to the nest or fledged young; non-reproductive owls either eat or cache the mice. A minimum of four mice (Peromyscus spp. or Mus musculus) was used to determine whether owls were nesting or offspring had been successfully produced. Owl pairs were usually visited at least twice to determine nesting status. Nesting pairs were revisited later in the season to determine the number of fledged young.

Capture

Owls were captured and marked after their reproductive status had been determined. Several capture techniques were used, including a noose pole (Forsman 1983), baited mist net, dip net and, occasionally, by hand. Handling of captured owls was always less than 20 minutes. Locking aluminum bands provided by the U.S. Fish and Wildlife Service (USFWS) were placed on the tarso-metatarsus of each captured Spotted Owl to verify the identity of individual owls during recaptures. Colored plastic leg bands developed by Eric Forsman (pers. comm.) were modified with colored vinyl tabs and placed on the opposing tarso-metatarsus in order to identify individuals without recapturing (see Franklin et al. 1987 for details).

Indentifying individual owls marked with USFWS leg bands in previous years required recapturing to check band numbers. Band loss was assumed to be zero. The identity of owls detected at night was either inferred by the position of the owl relative to known Spotted Owl territories or by sight identification of color-marked individuals. Color-banded individuals were positively identified by re-sighting color combinations within a mean of 17.3 minutes (n = 154 resights, SD = 21.3, median = 8 minutes) after the individuals had been located; 56.5% of the resightings occurred within ten minutes.

Determining Sex and Age

The sexes of adult and subadult Spotted Owls were distinguished by calls and general behavior. Males emit lower-pitched calls (Forsman et al. 1984). However, fledglings could not be accurately sexed.

Spotted Owls were aged by plumage characteristics. Three age categories were established: fledgling, sub-adult, and adult. Fledglings possess gray, downy body plumage and retrices with triangular, white tips through their first summer. Subadults possess typical, adult-like body plumage but retain the white tipped retrices until after their third summer (Forsman 1981). Adults have retrices with rounded and mottled tips. Molt of the retrices occurs every two years (Forsman 1981). Thus, known ages or minimum ages, in the case of existing adults, were determined using plumage condition and timing of the molt.

Data Analysis

Means and variances for reproductive data were calculated using formulae for a discrete frequency distribution (Zar 1984:31). Confidence limits for proportions were calculated using a relationship between the F distribution and the binomial distribution (Zar 1984:378).

Differences in proportions were tested using chi-square tests of homogeneity (Sokal and Rolf 1981:724; Zar 1984:49) on the raw counts used to calculate the proportions. Mann-Whitney U-tests (Sokal and Rolf 1981:433; Zar 1984:138) were used for pair-wise comparisons.

Annual survival rates for banded juveniles, subadults and adults were estimated using empirical methods. We also estimated survival rates for adults using Jolly-Seber (J-S) mark/recapture methods. In the empirical method, annual survival rates were calculated as:

 $M_{t+l}/M_{< t} \qquad \text{where} \qquad 1) \,\, M_{t+l} \,\, \text{ was the number of previously marked territorial occupants which were identifed and still alive in time $t+1$; and}$

2) $M_{< t}$ was the number of marked territorial occupants identified (by capture or resight) at or before time which were subsequently surveyed for in time t+1.

This method assumed that an owl was dead when it was either replaced on its territory by another owl or it went undetected for two or more years. This method also assumed that an individual was strongly faithful to its territory. J-S estimates for adults were calculated using the Jolly-Seber capturerecapture model for open populations (Jolly 1965, Seber 1965) which allows for both losses from and gains to the population between sampling periods. We calculated J-S estimates using model A (the standard Jolly-Seber model) in the computer program JOLLY (Brownie et al. 1986). For the five-year capture period (1984-1988), the Jolly-Seber model calculated survival rates only for the first three years. We also estimated survival rates for juveniles carrying radio-transmitters in 1983 and 1984 from data in Gutiérrez et al. (1985) and using the "exposure-day" model in computer program MICROMORT (Heisey and Fuller 1985). We did not include birds whose transmitters had failed except for one male who was recaptured on the WCSA in 1986.

Turnover rates were calculated as the proportion of marked adult and subadult owls replaced on their territories by another individual or found missing from their territories for ≥ 2 years. Turnover rate was, therefore, a function of subadult mortality, adult mortality, movements of birds between territories and reoccupation and abandonment of territories. This differed from calculations in previous reports which included only replacements. Data for 1985 through 1987 were re-calculated to conform to the current definition of turnover rate.

The study population, from which statistical inferences are drawn (Tacha et al. 1982), is defined in the Results section for each type of information gathered because of the varying time periods and study areas used. The target population, to which statistical inferences are applied (Tacha et al. 1982), is for all Northern Spotted Owls in the Douglas-fir biome in Del Norte, Siskiyou, Humboldt and Trinity counties in northwestern California. Time periods are specified in the Results and Discussion sections.

RESULTS

Surveys

Eighty-eight territories previously occupied by Northern Spotted Owl were surveyed on the RSA and WCSA in 1988 (Table 1, Figures 1 and 2). Owls were detected at 75 (85.2%) and reproduction was assessed at 66 (75.0%) of the territories surveyed (Table 1). We determined that six territories were unoccupied on the WCSA. Seven territories on the RSA were incompletely surveyed because of access problems, 'primarily from

Table 1. Number of Northern Spotted Owl territories surveyed, occupied and checked for reproduction in 1988 on the Willow Creek Study Area (WCSA) and Regional Study Area (RSA), northwest California.

	Study Area			
No. Territories:	WCSA	RSA	Combined	
Surveyed	43	45	88	
Found Occupied By:				
Pairs	35	30	65	
Males	2	7	9	
Females	0	1	1	
Total	$\frac{0}{37}$	$\frac{1}{38}$	75	
Checked For Reproduction				
Where Occupied By:				
Pairs	35	27	62	
Single Males	2	2	4	
Single Females	0	0	0	
Total	37	29	$\frac{0}{66}$	

Table 2. Sex-specific distribution of adult and subadult Northern Spotted Owls located and identified to age-class in 1988 on the Willow Creek Study Area (WCSA) and Regional Study Area (RSA), northwest California.

		WCSA	RSA	Combined
Sex	Age Class	n (%)	n (%)	n (%)
Male	Adult Subadult Combined	$\begin{array}{ccc} 34 & (94.4) \\ 2 & (5.6) \\ \hline 36 & (100.0) \end{array}$	26 (92.9) 2 (7.1) 28 (100.0)	60 (93.8) 4 (6.2) 64 (100.0)
Female	Adult Subadult Combined	$\begin{array}{ccc} 28 & (80.0) \\ 7 & (20.0) \\ \hline 36 & (100.0) \end{array}$	$\begin{array}{ccc} 22 & (91.7) \\ \underline{2} & (8.3) \\ 24 & (100.0) \end{array}$	$\begin{array}{cc} 50 & (84.7) \\ \frac{2}{59} & (15.3) \\ \hline (100.0) \end{array}$
Combined	Adult Subadult Combined	$\begin{array}{cc} 62 & (87.3) \\ 2 & (12.7) \\ 71 & (100.0) \end{array}$	$ \begin{array}{ccc} 48 & (92.3) \\ \frac{4}{52} & (7.7) \\ \hline 100.0) \end{array} $	110 (89.4) 13 (10.6) 123 (100.0)

private landowners. We found a total of 41 juveniles Spotted Owls which had fledged; 26 on the WCSA and 15 on the RSA.

Sex and Age-Class Distribution

The sex and age-class distributions for Northern Spotted Owls examined on the WCSA, and RSA (Table 2) were not significantly different ($X^2 = 1.67$, 3 df, P = 0.64). Overall, of the 123 owls found which were identified to age-class, 10.6% were subadults (Table 2). Although the percentage of subadult females (15.2%) was twice that of subadult males (6.2%), the difference was not significant ($X^2 = 2.63$, 1 df, P = 0.10).

Abundance and Density in the Willow Creek Study Area

Within the WCSA, 567 hours of survey effort were devoted to point, walk-in and cruise surveys (Table 3). As a result, 37 territories were identified as occupied within the WCSA in 1988 (Figure 1, Appendix 1). Thirty-five territories were occupied by pairs of Spotted Owls while 2 (5.4%) were occupied by unpaired males for a total of 72 adult and subadult Spotted Owls. Sixtynine (95.8%) of the Spotted Owls located within the WCSA were

Table 3. Effort expended in surveying the Willow Creek Study Area, northwest California, from 1985 through 1988.

		Year			Total
Variable	1985	1986	1987	1988	
Hours Spent S	urveying	•			
Point	169.0	82.4	163.4	202.8	617.6
Walk-in	200.8	229.7	324.9	277.4	1032.8
Cruise	79.0	24.9	84.2	86.5	274.6
Total	448.8	337.0	572.5	566.7	1925.0
Number Of Sur	veys:				
Point	469	206	496	778	1949
Walk-in	89	110	134	141	474
Cruise	36	15	47	48	146
Total	594	331	677	967	2569
No. Calling					
Stations Used	317	111	321	540	

Table 4. Proportion of Northern Spotted Owl pairs checked for reproductive activity before 31 May which nested in the Willow Creek Study Area (WCSA) and Regional Study Area (RSA), northwest California, from 1985 through 1988. Ninety-five percent confidence intervals are in parentheses.

	No. Pairs	Propo	Proportion of Pairs Nesting			
Year	Checked (WCSA, RSA)	WCSA	RSA	Combined ^a		
1985	42 (42,18)	(0.44 - 0.79)	$\begin{pmatrix} 0.50 \\ (0.29 - 0.71) \end{pmatrix}$	$\begin{pmatrix} 0.57 \\ (0.43-0.70) \end{pmatrix}$		
1986	$ \begin{array}{c} 41 \\ (29,12) \end{array} $	$\begin{pmatrix} 0.69 \\ (0.52 - 0.83) \end{pmatrix}$	$\begin{pmatrix} 0.92 \\ (0.66-1.00) \end{pmatrix}$	$\begin{pmatrix} 0.76 \\ (0.62 - 0.86) \end{pmatrix}$		
1987	41 (25,16)	(0.42 - 0.76)	$\begin{pmatrix} 0.81 \\ (0.58-0.95) \end{pmatrix}$	$\begin{pmatrix} 0.68 \\ (0.54 - 0.80) \end{pmatrix}$		
1988	45 (31,14)	(0.55 - 0.84)	$\begin{pmatrix} 0.79 \\ (0.53-0.94) \end{pmatrix}$	$\begin{pmatrix} 0.73 \\ (0.60-0.84) \end{pmatrix}$		

aWCSA and RSA not significantly different for 1985 ($X^2 = 0.66$, 1 df, P = 0.42) 1986 ($X^2 = 0.59$) and RSA not significantly different for 1985 ($X^2 = 0.66$, 1 df, P = 0.42) 1986 ($X^2 = 0.59$)

Table 5. Proportion of nesting pairs of Northern Spotted Owls which fledged young in the Willow Creek Study Area (WCSA) and Regional Study Area (RSA), northwest California, from 1985 through 1988. Ninety-five percent confidence intervals are in parentheses.

	No. Pairs	Proportion of Nesting Pairs Which Fledged Young		
Year	Nesting (WCSA, RSA)	WCSA	RSA	Combined ^a
1985	24	0.73	0.67	0.71
	(15, 9)	(0.49-0.90)	(0.35-0.91)	(0.52-0.85)
1986	31	0.55	0.91	0.62
	(20, 11)	(0.35-0.74)	(0.64-1.00)	(0.49-0.74)
1987	28	0.67	0.92	0.79
	(15, 13)	(0.42-0.86)	(0.68-1.00)	(0.62-0.90)
1988	33	0.86	0.91	0.88
	(22, 11)	(0.68-0.96)	(0.64-1.00)	(0.74-0.96)

^aWCSA and RSA not significantly different for 1985 ($X^2 = 0.12$, 1 df, P = 0.73), 1987 ($X^2 = 2.72$, 1 df, P = 0.10) or 1988 ($X^2 = 0.14$, 1 df, P = 0.71) but significantly different for 1986 ($X^2 = 4.19$, 1 df; P = 0.04).

individually identified either by capturing them (n = 16) or resighting their color-band combinations (n = 53). Analysis of crude and ecological densities for 1985 through 1988 were reported in Franklin et al. (in press).

Reproduction

Proportion of Population Nesting and Fledging Young

The proportion of pairs checked annually for reproduction which nested in 1985 through 1988 (Table 4) was not significantly different among years ($X^2 = 3.46$, 3 df, P = 0.33). We used only those pairs checked for reproduction before 31 May, which we considered the end of the nesting period. For the four years combined, 67.8% of the pairs nested (n = 169 pairs; 95% C.I. = 61.5 - 73.7%). Annual estimates for the WCSA were not significantly different from estimates for the RSA (Table 4).

There was much greater variability between annual estimates of the proportion of nesting pairs which fledged young in the WCSA and RSA; a significantly higher proportion of nesters

Table 6. Proportion of Northern Spotted Owl pairs checked for reproductive activity which fledged young in the Willow Creek Study Area (WCSA) and Regional Study Area (RSA), northwest California, from 1985 through 1988. Ninety-five percent confidence intervals are in parentheses.

	No. Pairs	Proport	ion of Pairs Fledgi	ng Young
Year	Checked (WCSA, RSA)	WCSA	RSA	Combined ^a
1985	48	0.41	0.29	0.35
	(27,21)	(0.29-0.58)	(0-13-0.49)	(0.24-0.48)
1986	50	0.36	0.50	0.42
	(30, 20)	(0.22-0.53)	(0.30-0.70)	(0.30-0.55)
1987	56	0.32	0.48	0.39
	(31, 25)	(0.19-0.50)	(0.31-0.66)	(0.28-0.51)
1988	62 (35, 27)	0.54 (0.39-0.69)	0.37 $(0.22-0.55)$	0.47 (0.36-0.58)

^aWCSA and RSA not significantly different for 1985 ($X^2 = 0.76$, 1 df, P = 0.38), 1986 ($X^2 = 0.88$, 1 df, P = 0.34), 1987 ($X^2 = 1.22$, 1 df, P = 0.23) or 1988 ($X^2 = 1.82$, 1 df, P = 0.18).

fledged young in the RSA in 1986 (Table 5). However, estimates for 1985 through 1988 (Table 5) were not significantly different among years for the two study areas combined ($X^2 = 4.22$, 3 df, P = 0.24). Overall, the proportion of nesting pairs which fledged young on both study areas was 76.7% for all four years (n = 116; 95% C.I. = 69.4 - 83.0%).

The proportion of pairs checked which fledged young in 1985 through 1988 (Table 6) was not significantly different among years ($X^2 = 1.56$, 3 df, P = 0.67). For the four years combined, 41.2% of the pairs fledged young (n = 216; 95% C.I. = 35.6 - 47.0%). There was no significant difference between annual estimates for the WCSA and RSA (Table 6).

Because we did not find significant differences in reproduction in northwest California for the period 1985-1988, all paired females which could be aged as either adults (n=132) or subadults (n=33) were used to examine differences in reproductive characteristics between the two age classes (Table 7). The proportion of females nesting and fledging young were

Table 7. Reproductive characteristics of paired subadult and adult female Northern Spotted Owls of known age on the Willow Creek Study Area and Regional Study Area, northwest California, from 1985 through 1988. Ninety-five percent confidence intervals are in parentheses.

			Proportion		
Age class	n ^a	Mean number of young fledged ^b	Nesting ^c	Fledging young ^d	
Subadult	34	0.41 (0.12-0.70)	0.36 (0.23-0.52)	0.24 (0.12-0.39)	
Adult	144	0.72 (0.58-0.86)	0.64 (0.57-0.71)	0.46 (0.39-0.53)	
Combined	178	0.66 (0.54-0.79)	0 . 5 9 (0.52-0.65)	0.42 (0.35-0.48)	

 $^{^{}a}_{n}$ n = 132 adults and 33 subadults for proportion nesting.

significantly greater for adults (0.64 and 0.46, respectively) than for subadults (0.36 and 0.24, respectively).

Reproductive Output

In 1988, a mean of 0.66 young were fledged per pair (Table 8). This estimate was not significantly different than estimates for 1985, 1986 or 1987 (Kruskal-Wallis test, H = 0.41, P = 0.94). There were no significant differences in the observed variation between the WCSA and RSA for any year (Table 8). For the four years combined, a mean of 0.65 young were fledged, per pair (n = 216, 95% C.I. = 0.53 - 0.76). Mean number of young fledged per adult female (0.72) was significantly greater than for subadult females (0.41; Table 7). For modelling purposes, mean fecundity (number of female young fledged per female) for adults and subadults was calculated assuming a 1:1 sex ratio, by dividing the number of young fledged per pair by two prior to calculating means and standard errors. Mean fecundity was 0.36 (SE = 0.04, n = 144) for adults and 0.21 for subadults (SE = 0.07, n = 34).

^bAdult and subadult age classes significantly different (Mann-Whitney U Test; Z = -2.09, P = 0.04)

cAdult and subadult age classes significantly different $(X^2 = 8.56, 1 \, df, P = 0.01)$. dAdult and subadult age classes significantly different $(X^2 = 5.63, 1 \, df, P = 0.02)$.

Table 8. Mean number of young fledged per pair of Northern Spotted Owls in the Willow Creek Study Area (WCSA) and Regional Study Area (RSA), northwest California, from 1985 through 1988. Ninety-five percent confidence intervals for means are in parentheses.

	No. Pairs	Mean Nu	imber of Young Fled	lged per Pair
Year	Checked (WCSA, RSA)	WCSA	RSA	Combined ^a
1985	(27, 21)	0.67 (0.32-1.01)	$\begin{pmatrix} 0.52 \\ (0.14-0.91) \end{pmatrix}$	$\begin{pmatrix} 0.60 \\ (0.35 - 0.86) \end{pmatrix}$
1986	(30, 20)	$\begin{pmatrix} 0.57 \\ (0.25 - 0.88) \end{pmatrix}$	$\begin{pmatrix} 0.80 \\ (0.42 - 1.18) \end{pmatrix}$	$ \begin{array}{c} 0.66 \\ (0.41 - 0.90) \end{array} $
1987	(31, 25)	$\begin{pmatrix} 0.55 \\ (0.23 - 0.86) \end{pmatrix}$	$\begin{pmatrix} 0.80 \\ (0.44-1.15) \end{pmatrix}$	$\begin{pmatrix} 0.66 \\ (0.43 - 0.90) \end{pmatrix}$
1988	(35, 27)	$ \begin{array}{c} 0.74 \\ (0.47-1.02) \end{array} $	$\begin{pmatrix} 0.56 \\ (0.24 - 0.87) \end{pmatrix}$	$\begin{pmatrix} 0.66 \\ (0.46 - 0.87) \end{pmatrix}$

^aWCSA and RSA not significantly different (Mann-Whitney U Test) for 1985 ($Z=0.68,\ P=0.50$), 1986 ($Z=-0.95,\ P=0.34$), 1987 ($Z=-1.11,\ P=0.27$), or 1988 ($Z=1.03,\ P=0.30$).

Table 9. Mean productivity of Northern Spotted Owl pairs in the Willow Creek Study Area (WCSA) and Regional Study Area (RSA), northwest California, from 1985 through 1988. Ninety-five percent confidence intervals for means are in parentheses.

	No. Pairs		Mean Productivity	
Year	Checked (WCSA, RSA)	WCSA	RSA	Combined ^a
1985	(12, 5)	1.63 (1.33-1.94)	1.83 (1.42-2.25)	1.71 (1.46-1.95)
1986	2 1 (11, 10)	1.55 (1.22-1.87)	1.60 (1.25-1.94)	1.57 (1.33-1.81)
1987	(10, 12)	1.70 (1.38-1.90)	(1.37-1.96)	1.68 (1.46-1.90)
1988	(19, 10)	(1.10-1.64)	1.50 (1.13-1.87)	1.44 (1.19-1.63)

 $^{\rm a}WCSA$ and RSA not significantly different (Mann-Whitney U Test) for 1985 (Z = -0.76, P = 0.45), 1986 (Z = -0.21, P = 0.84), 1987 (Z = 0.12, P = 0.90), or 1988 (Z = -0.78, P = 0.43).

Table 10. Annual turnover rates from 1984-85 through 1987-88 in territories occupied by banded male and female Northern Spotted Owls in northwest California.

			Turnover Rate						
		No. Banded	WCSA RSA		ombined				
Sex	Year	Birds Checked (WCSA, RSA)			P	(95% CI)			
Males	1984-85 1985-86 1986-87 1987-88	17 (-, -) ^a 39 (29, 10) 45 (35, 10) 54 (32, 22)	0.10 0.20 0.13	0.10 0.10 0.05	$0.10 \\ 0.18$	(0.02-0.33) (0.04-0.22) (0.09-0.30) (0.04-0.19)			
Females	1984-85 1985-86 1986-87 1987-88	14 (-, -) ^a 36 (28, 8) 39 (31, 8) 50 (31, 19)	0.14 0.26 0.29	0.13 0.13 0.21	$0.14 \\ 0.23$	(0.01-0.30) (0.06-0.27) (0.13-0.37) (0.16-0.38)			
Both	1984-85 1985-86 1986-87 1987-88	31 (-, -) ^a 75 (57, 18) 84 (66, 18) 104 (63, 41)	0.12 0.23 0.21	0.11 0.11 0.12	$0.12 \\ 0.20$	(0.03-0.23) (0.06-0.20) (0.13-0.29) (0.12-0.25)			

^aSample pooled across WCSA and RSA.

Mean productivity in 1988 was 1.44 young per breeding female (Table 9). The 1988 estimate was not significantly different from estimates for 1985, 1986 and 1987 (Kruskal-Wallis test, H = 5.57, P = 0.13). Little annual variation was observed between the two study areas (Table 9). For the four years combined, a mean of 1.57 young were fledged per pair which produced young (n = 89, 95% C.I. = 1.46 - 1.68).

Site and Mate Fidelity

Overall, there was a 12.3% mean annual turnover rate for male and 20.1% turnover rate for female territory holders on the WCSA and RSA from 1984-85 through 1987-88 (Table 10). Male (9.3%) and female (26.0%) turnover rates for 1988 were significantly different ($X^2 = 5.08$, 1 df, P = 0.02). However, male and female rates were not significantly different for the other years ($X^2 = 0.19 - 0.36$, 1 df, P = 0.55 - 0.66). While male rates have varied between 9% and 18%, female rates have shown a steady increase between 1984-85 and 1987-88 (Table 10). One male banded

Table 11. Proportion of territories in the Willow Creek Study Area, northwest California, which were occupied by unpaired Northern Spotted Owls from 1985 through 1988. Ninety-five percent confidence intervals are in parentheses.

	No. of	Proportion of	Percent (n) of Single Territories Containing				
Year	Territories Checked	Territories with Single Birds	Males	Females			
1985 ^a	36	0.17 (0.07-0.30)	88 (6)	12 (1)			
1986 ^b	34	0.09 (0.02-0.21)	1003)	0 (0)			
1987	36	0.14 (0.06-0.27)	80 (4)	20 (1)			
1988	37	0.05 (0.01-0.16)	100(2)	0 (0)			

^aData from Franklin et al. (1986). ^bData from Franklin et al. (1987).

in 1982 has occupied the same territory for at least seven years while a female banded as a subadult in 1981 has occupied the same territory for eight years. The percentage of adults in birds newly recruited into the WCSA population has increased from 28.6% (= 2/7) in 1986 to 41.7% (= 5/12) in 1987 and 1988. The remainder of recruitment has been subadults.

Of 126 pair bonds observed from 1985 through 1988, three have ended in divorce for a divorce rate of 2.4%. One of the divorces was observed in 1986 (Franklin et al. 1987) and two were observed in 1988. Two females divorced their mates who remained single on their territories after the divorce. One of the divorced males dissappeared after remaining single for one year (NFMCC territory in Appendix 1) while the other divorced male has remained single for two years (GRAYC territory in Appendix 1). The third divorce was mutual with each of the divorced mates pairing with other owls in separate territories.

Occupancy of Territories

The percentage of territories in the WCSA occupied by unpaired Spotted Owls in 1988 was 5.4 % and was not significantly different than estimates for 1985, 1986 or 1987 ($X^2 = 2.79$, 3 df, P = 0.43; Table 11). A combined estimate of 12.6% was calculated for 1985 through 1988 (n = 143, 95% C.I. = 0.08 - 0.19). Annually, 80% to 100% of the unpaired owls were males (Table 11).

A total of 43 territories have been documented on the WCSA between 1985 and 1988 (Appendix 1). The number of occupied territories on the WCSA have remained relatively constant at 36 territories occupied in 1985, 33 in 1986, 36 in 1987 and 37 in 1988 (Appendix 1). However, only 24 (55.8%) of the 43 territories were occupied by pairs every year for the four-year period.

Four territories were abandoned in 1988 (BURRS, FOURM, HENRW and SPIKE; Appendix 1). Prior to 1988, single males occupied two of the territories while pairs occupied the other two (HENRW and SPIKE), portions of which were logged in 1987. One territory (MAHAL) abandoned by a pair of subadults in 1987 was re-occupied in 1988 by a single, subadult male. In addition, four new territories were apparently established on the WCSA (HORSE, MINGC, PANTH and PONYC; Appendix 1). Birds previously located on the WCSA made up both of the occupants in HORSE and one of the occupants in both MINGC and PONYC. PANTH was occupied by a pair of adults new to the WCSA. Rates of occupation between 1987 and 1988 on the WCSA were not calculated because we were uncertain whether the four new territories were "ephemeral" (birds occupying areas for only a year before disappearing, e.g CHINA and HENRW territories in 1987). An additional one to two years of research will probably be required to put the population flux seen in 1988 into perspective.

Movements Between Territories

Inter-territorial movements on the WCSA involved subadult (n = 4) and adult (n = 6) owls leaving established territories and either replacing other individuals on established territories, or establishing new territories with other birds. Nine such movements (5 by adults) were observed in 1988 compared with only one previously observed by an adult in 1986 (Franklin et al. 1987). One of the movements included an adult female migrating 4.5 km (2.8 mi) into the WCSA from a territory in the RSA. All of the movements were associated with new pair bonds being formed after the movement. In addition, we documented in 1986 and 1987 5 dispersals within the WCSA by juveniles born on the WCSA in 1985 (n = 4) and 1986 (n = 1). All of these dispersals resulted in the formation of pair bonds on established territories. As a subadult male, one of the juveniles successfully fledged 2 young 2.3 km from his natal territory. Although no dispersals were observed in 1988, 4 of the 5 dispersing juveniles still occupied territories in the WCSA.

Eighty percent of the observed dispersals by juveniles were by males while 83.3% of inter-territorial movements by adults were by females (Figure 3A). Movements by subadults were equally divided between the two sexes, Eighty percent of the juvenile dispersals were observed in 1986, 20% in 1987 and none in 1988 (Figure 3B). All of subadult and 83.3% of adult inter-

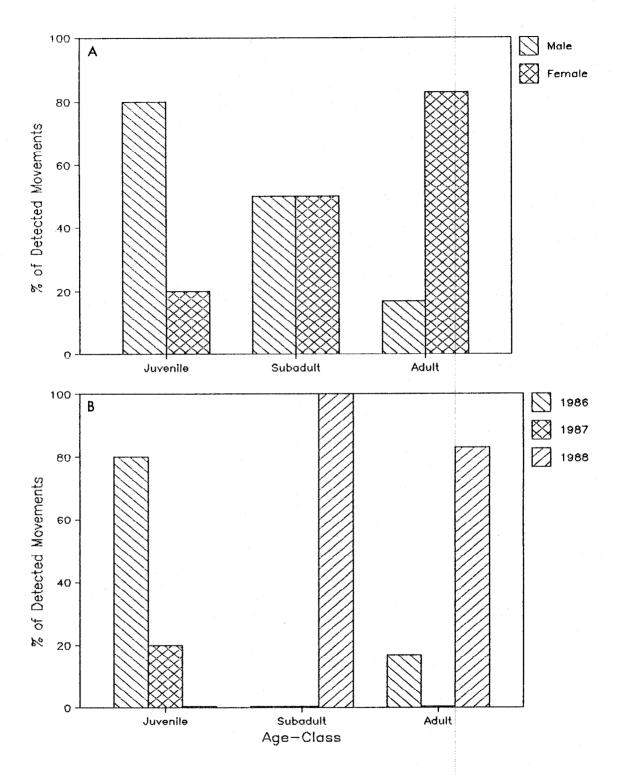


Figure 3. Age-class distributions of inter-territorial movements by banded Northern Spotted Owls for (A.) sex and (B.) year on the Willow Creek Study Area, northwest California, from 1986 through 1988.

territorial movements were observed in 1988. We did not include the one subadult observed in 1985 (Franklin et al. 1986) because it was a "floater" and not an inter-territorial movement according to our definition.

Successful dispersal distances by juveniles observed on the WCSA averaged 7.2 km (SD = 4.2, range = 2.3 - 11.6 km). Distances moved by subadults averaged 4.4 km (SD = 2.9, range = 2.5 - 8.4 km) while adults averaged 3.5 km (SD = 3.3, range = 0.6 - 9.7 km). Distances moved by the three age-classes were not significantly different (One-way ANOVA; F-ratio = 1.62, P = 0.24; Figure 4).

Annual Survival

A total of 513 identifications (captures, recaptures and resightings) of individuals have been made on the WCSA and RSA from 1984 through 1988 (Table 12), not including multiple recaptures and re-sightings of individuals within the same year. Data on individual identifications were used to estimate survival rates using empirical and Jolly-Seber models. Because banding data on subadults and juveniles was collected only from 1984-85 through 1987-88, adult survival rates were calculated for this time period to make comparisons (Table 13), as well as from 1984-85 through 1987-88.

Table 12. Number of Northern Spotted Owls identified in northwest California from 1984 through 1988. New birds were owls that had not been previously banded; old birds were owls that had been previously banded.

	No. New	Birds	Captured	N	G 1		
Year	Ad/Subad	Juv.	Total	Recap.	Resight	Total	Grand Total
1984	29	17	46	3	0	3	49
1985	54	17	70	22	0	22	93
1986	10	17	26	54	0	54	81
1987	48	29	79	42	18	60	137
1988	18	36	54	13	86	99	153
Total	159	116	275	134	104	238	513

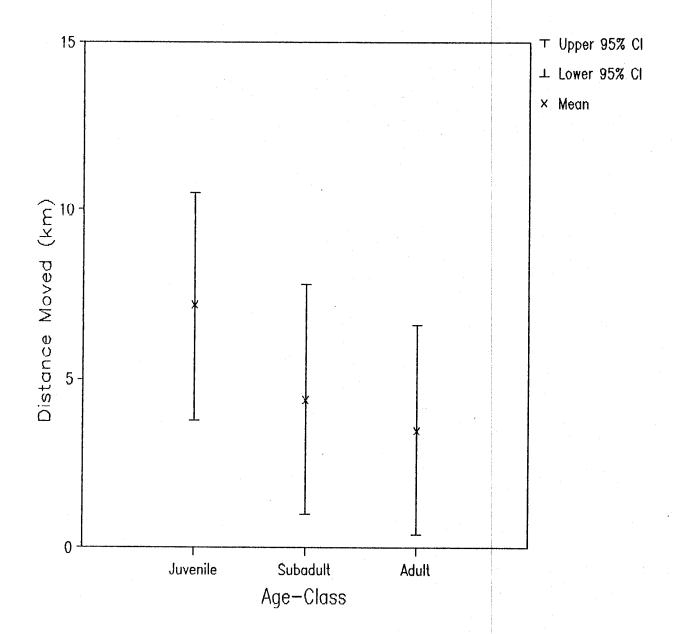


Figure 4. Mean distances moved by banded juvenile, subadult and adult Northern Spotted Owls on the Willow Creek Study Area, northwest California, from 1986 through 1988.

Table 13. Empirical estimates of annual survival rates for banded juvenile, subadult and adult Northern Spotted Owls in northwest California from 1985 through 1988. Sample sizes are in parentheses.

			Year				Overall			
Age Class	Sex	198:	5-86	1986	5-87	1987	7-88	198	5-88	95% CI
Juvenile	M&1	F 0.18	3 (17)	0.06	(17)	0.00	(29)	0.06	(63)	0.02-0.14
Subadult	M F M&F	0.00 0.88 0.78	(1) (8) (9)	0.67 0.60 0.63	(3) (5) (8)	0.80 0.89 0.86	(5) (9) (14)	0.67 0.87 0.77	(9) (22) (31)	0.35-0.90 0.63-0.94 0.62-0.89
Adult	M F M&F	0.93 0.86 0.90	(43) (29) (72)	0.95 0.84 0.91	(42) (32) (74)	0.98 0.88 0.94	(53) (43) (96)	0.960 0.870 0.920	(104)	0.92-0.98 0.80-0.92 0.88-0.95

<u>Juveniles</u>

Annual survival rates for radio-transmittered juveniles were 0.14 in 1983 (SE = 0.09, n = 9 individuals and 1691 radiodays) and 1984 (SE = 0.10, n = 7 individuals and 1284 radiodays). Survival rates estimated from banding data decreased from 0.18 in 1985-86 to 0.00 in 1987-88 (Table 13) with an overall rate for the four-year period of 0.06 (SE = 0.03, n = 63).

Subadults

The overall annual survival rate for subadult males from 1985 through 1988 was 0.67 (SE = 0.16, n = 9) which was not significantly different ($X^2 = 0.84$, 1 df, P = 0.36) from the rates of 0.87 (SE = 0.08, n = 22) for subadult females (Table 13). Annual rates for subadults (both sexes combined) also were not significantly different ($X^2 = 1.57$, 2 df, P = 0.46). The overall rate of 0.77 (SE = 0.07, n = 31) for subadults (years and sexes combined) was significantly greater than the overall rate for juveniles ($X^2 = 5.87$, 1 df, P = 0.02).

Adults

Empirical and J-S estimates for adult male and female survival rates were comparable (Figure 5). Capture histories from 71 males were used in the J-S analysis. J-S estimates for adult male survival ranged from 1.00 (SE = 0.02) in 1984-85 to

0.90 (SE = 0.06) in 1986-87 with an overall rate (all years combined) of 0.96 (SE = 0.02) for the period of 1984 through 1987 (Figure 5). Empirical rates ranged from 0.93 (SE = 0.04) in 1985-86 to 1.00 in 1984-85 with an overall rate (all years combined) of 0.96 (SE = 0.02, n = 153) for the period of 1984 through 1988. Empirical annual rates for adult males were not significantly different ($X^2 = 1.50$, 3 df, P = 0.47). The overall empirical estimate of 0.96 (SE = 0.02) for adult males from 1985 through 1988 was significantly higher ($X^2 = 12.35$, 1 df, P < 0.001) than the comparable rate for subadult males (Table 13).

Capture histories from 64 females were used in the J-S analysis. J-S estimates for adult female survival ranged from 0.77 (SE = 0.11) in 1984-85 to 0.88 (SE = 0.07) in 1986-87 with an overall rate (all years combined) of 0.84 (SE = 0.05) for the period of 1984 through 1987 (Figure 5). Empirical rates ranged from 0.84 (SE = 0.06) in 1986-87 to 0.93 (Sk = 0.07) in 1984-85 with an overall rate (all years combined) of 0.87 (SE = 0.03, n = 118) for the period of 1984 through 1988. Empirical annual rates for adult females were not significantly different ($X^2 = 0.26$, 2 df, P = 0.88). The overall empirical estimate of 0.87 (SE = 0.03) for adult females from 1985 through 1988 was not significantly different ($X^2 = 0.33$, 1 df, P = 0.57) than the comparable rate for subadult females (Table 13). The overall empirical estimate for adult females calculated for 1984-85 through 1987-88 was significantly lower ($X^2 = 6.50$, 1 df, P = 0.01) than comparable rates for adult males.

Since inter-territorial movements may have affected the assumptions underlying calculation of empirical survival rates on the WCSA, we examined empirical rates calculated from the RSA and WCSA (where we were able to detect and correct for movements). The empirical rate of 0.89 (n = 26) for adult females on the WCSA was not significantly different ($X^2 < 0.01$, 1 df, P = 0.98) from a rate of 0.88 (n = 17) for adult females on the RSA. In addition, the empirical rate of 0.97 (n = 29) for adult males on the WCSA was not significantly different ($X^2 = 0.48$, 1 df, P = 0.49) from a rate of 1.00 (n = 24) for adult males on the RSA.

Effects of Fires

Five territories in the RSA, which contained pairs of Northern Spotted Owls, were impacted by fires in the fall of 1987. Three of the territories were within the Titus fire on the Klamath National Forest and two were burned by smaller fires on the Shasta-Trinity National Forest. All of the territories experienced light to moderate understory burns. The conifer and hardwood overstories had remained intact where the owls were located although much of the ground cover and hardwood midstories had been removed by fires.

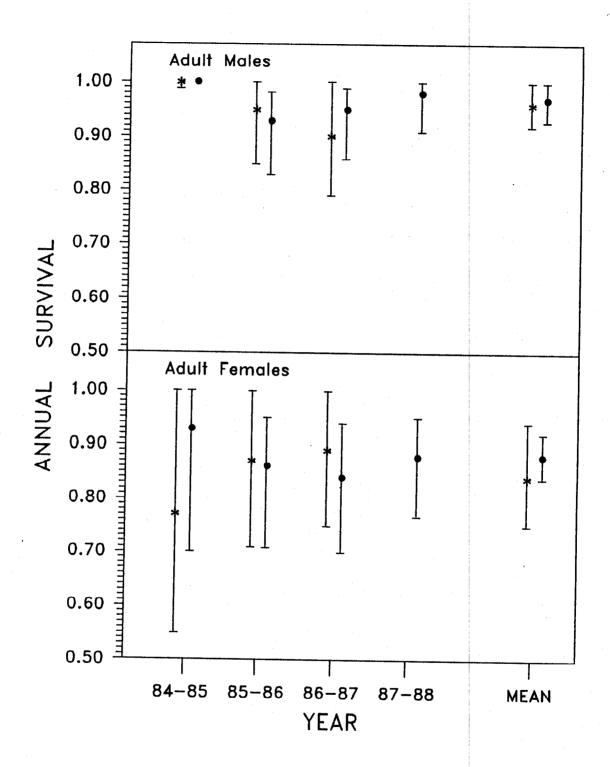


Figure 5. Mean survival estimates, with 95% confidence intervals (bars), for adult male and female Northern Spotted Owls in northwest California from 1984 through 1988. Estimates calculated with empirical (dots) and Jolly-Seber (stars) methods.

Of the 10 adults located and banded on the five territories in 1987, 9 (90%) survived to 1988; an adult female was replaced by a subadult on one territory. In addition, three (60%) of the pairs nested and two fledged one young each for a mean of 0.40 young fledged per pair.

DISCUSSION

The decline in the adjusted territorial population on the WCSA in 1987 (Franklin and Gutiérrez 1988) was apparently a temporary shift in abundance. The number of occupied territories and the number of Spotted Owls has remained relatively stable on the WCSA for the past four years. However, only about half of these territories have been consistently occupied by pairs over this time span. In addition, the population on the WCSA is currently undergoing some manner of social change. In 1988, we observed increased divorces, a nine-fold increase in interterritorial movements by adults and subadults from the previous three years, and the formation of four new territories. The amount of mature and old-growth habitats removed by logging on the WCSA has increased from 0.5 km² removed between 1985 and 1986 to 4.0 km² over the next two years (Franklin et al., in press) yielding an apparent increase in ecological density. Reduction and fragmentation of Spotted Owl habitat may have the short-term effect of forcing birds to move in order to survive. Female Sparrowhawks (Accipiter nisus) showed a strong tendency to remain on territories with high habitat quality and to move from territories with low habitat quality (Newton and Marquiss 1982).

Prior to 1988, the WCSA population exhibited a high degree of site and mate fidelity (Franklin and Gutiérrez 1988, Franklin et al. 1986, 1987). Presumably, it would be advantageous for Spotted Owls to maintain the same mate and territory as long as possible in order to maximize the chances of successfully rearing young and individual survival. Southern and Lowe (1968) hypothesized that intimate knowledge of a territory by Tawny Owls (Strix aluco) was an important factor in reproductive success and could override periods of prey shortages. Martin (1986) supported this view from a physiological basis hypothesizing that detailed knowledge of local topography was equally as important as the high sensory sensitivities which allow owls to be active at night. In Florida Scrub Jays (Aphelocoma coerulescens coerulescens), a high degree of mate fidelity was advantageous for reproductive output (Woolfenden and Fitzpatrick 1984). However, reproductive output on the WCSA was the highest in 1988 despite the increased movements.

Reproductive parameters for Spotted Owls in northwest California have remained stable over the four-year study period. Although we observed some geographic variation in reproductive variables between the WCSA and RSA, combined annual estimates for these variables also exhibited little variation among years.

Subadult females nested less frequently and produced fewer young than adult females.

Annual survival rates for adults have remained stable from 1985 through 1988. The decline reported in 1987 by Franklin and Gutiérrez (1988) was reversed in 1988. However, adult females have significantly lower survival rates than males. Nichols et al. (1980), Mertz (1971) and Knight and Eberhardt (1985) showed that the finite rate of population change was most sensitive to changes in adult survival in life table analyses of long-lived species with the high adult survival and low reproductive rates characteristic of the Spotted Owl. The demographic model for Spotted Owls by Lande (1988) used an adult female survival value of 0.92 and predicted a 4% decline in Spotted Owl populations. Inclusion of the lower value of 0.87 reported in this study would result in a greater rate of decline. Continued monitoring of adult survival may provide a useful index for predicting population trends and serve as an indicator for necessary changes in management strategies.

Survival rates estimated from banded juveniles should be considered minimum estimates because of the dispersal ability of juveniles (Gutiérrez et al. 1985, Miller and Meslow 1985). However, survival rates calculated from banded juveniles has not refuted the low rates calculated from transmittered juveniles.

The validation of the trends observed in Spotted Owl populations in northwest California will require additional years of research. However, if declines in abundance, annual survival and occupation of territories continue, there may be a serious problem in maintaining the viability of Spotted Owl populations.

Short-term conclusions on the changes observed in 1988 are difficult to make. An important factor to consider when dealing with long-lived species, such as the Spotted Owl, is that lag effects may occur. Current losses of habitat on the WCSA may not have an immediate effect on the population until several years later.

ACKNOWLEDGEMENTS

The study would not have been completed this year without the dedicated work of Christine Moen, Kendal Young and Marc Kasper. They worked many long hours in the field and contributed immeasurably to the success of this project with their initiative, expertise and unflagging good humor. We would particularly like to thank Pat 'Ranger' Ward of Humboldt State University, Gordon Gould of the California Department of Fish and Game and Barry Noon of Redwood Sciences Laboratory for their support and dedication. Without them the continuation of this project would not have been possible. We thank David Solis, Jack

Kahl, Jeff Mattison, Don Kudrna, Ann Chrisney, Marilyn Fox, Terry Davis and Larry Cabodi of the Six Rivers National Forest for their assistance in providing information and logistic support. We extend our gratitude to Pat Ward, Jim Heaney, Mark Andre, Cindy Levy, Kathy Nickell, Bruce Bingham, Peter Steele, George Kalisik, Jim Decker, Mark Williams, Eric Hopson, Terry Brumley and Cameron Barrows for their assistance and willingness to share information. We also thank Jim Hamby of the HSU Foundation for keeping the money flowing. Pat Ward kindly reviewed earlier drafts of this manuscript. Thanks to the Six Rivers National Forest which provided vehicles, the 'Red Rhino' was finally allowed a well deserved vacation to rust in peace.

LITERATURE CITED

- Brownie, C., J.E. Hines and J.D. Nichols. 1986. Constantparameter capture-recapture models. Biometrics 42:561-574.
- Caughley, G. 1977. Analysis of vertebrate populations. J. Wiley and Sons, London. 234 pp.
- Forsman, E.D. 1981. Molt of the Spotted Owl. Auk 98: 735-742.
- Forsman, E.D. 1983. Methods and materials for locating and studying Spotted Owls. U.S. For. Serv. Gen. Tech. Rep. PNW-12. 8pp.
- Forsman, E.D., E.C. Meslow and H.M. Wight. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildl. Monogr. 87. 64pp.
- Franklin, A., J.P. Ward, and R.J. Gutiérrez. 1986. Population ecology of the Northern Spotted Owl (Strix occidentalis caurina) in northwestern California: preliminary results, 1985. Unpubl. Prog. Rep. Project Work No. W-65-R-3 (554). Calif. Dept. Fish & Game. Sacramento, CA. 42pp.
- Franklin, A., J.P. Ward, and R.J. Gutiérrez. 1987. Population ecology of the Northern Spotted Owl (Strix occidentalis caurina) in northwestern California: preliminary results, 1986. Unpubl. Prog. Rep. Project Work No. W-65-R-4 (554). Calif. Dept. Fish & Game. Sacramento, CA. 29pp.
- Franklin, A. and R.J. Gutiérrez. 1988. Population ecology of the Northern Spotted Owl (Strix occidentalis caurina) in northwestern California: preliminary results, 1987. Unpubl. Prog. Rep. Calif. Dept. Fish and Game Project Work No. W-65-R-4 (554) and USDA For. Serv. Cooperative Research Agreement PSW-87-0011CA. 27pp.

- Franklin, A., J.P. Ward, R.J. Gutiérrez and G.I. Gould. In press. Density of Northern Spotted Owls in northwest California. J. Wildl. Manage.
- Gould, G.I., Jr. 1974. The status of the Spotted Owl in California. Unpubl. Tech. Rep., Calif. Dept. Fish and Game and USDA Forest Serv., Region 5. 34pp.
- Gould, G.I., Jr. 1977. Distribution of the Spotted Owl in California. Western Birds 8(4): 131-146.
- Gould, G.I., Jr. 1985. Management of Spotted Owls by the California Department of Fish and Game. Pages 21-26 in Gutiérrez, R.J. and A.B. Carey (eds.). Ecology and management of the spotted owl. U.S. For. Serv. Gen. Tech. Rept. PNW-185. 119pp.
- Grinnell, J. and A.H. Miller. 1944. The distribution of the birds of California. Pacific Coast Avifauna 27. 608pp.
- Gutiérrez, R.J., D.M. Solis and C. Sisco. 1984. Habitat ecology of the Spotted Owl in northwestern California: implications for management. Pages 368-373 in Proc. Soc. Amer. Foresters Natl. Conv., 16-20 Oct., 1983.
- Gutiérrez, R.J., J.P. Ward, A.B. Franklin, W. LaHaye and V. Meretsky. 1985. Dispersal ecology of juvenile Northern Spotted Owls (Strix occidentalis caurina) in northwestern California. Unpubl. Tech. Rep., USDA Forest Serv., Pacific NW Forest and Range Exper. Sta., Olympia, WA. 48pp.
- Heinrichs, J. 1984. The owl and the old growth. Amer. Forests 90:22-23;54-56.
- Heisey, D.M. and T.K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. J. Wildl. Manage. 49:668-674.
- Johnson, D.R. 1978. The study of raptor populations. Univ. Press of Idaho, Moscow. 57pp.
- Johnston, V.H. and J.P. Ryder. 1987. Divorce in Larids: a review. Colonial Waterbirds 10(1):16-26.
- Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225-247.
- Knight, R.R. and L.L. Eberhardt. 1985. Population dynamics of Yellowstone Grizzly Bears. Ecology 66:323-334.

- Kuchler, A.W. 1977. The map of the natural vegetation of California. Pages 909-938 in M. Barbor and J. Majors, eds. Terrestrial vegetation of California. John Wiley and Sons, New York. 1002pp.
- Lande, R. 1988. Demographic models of the Northern Spotted Owl (Strix occidentalis caurina). Oecologia 75:601-607.
- Martin, G.R. 1986. Sensory capacities and the nocturnal habit of owls (Strigiformes). Ibis 128:266-277.
- Mertz, D.B. 1971. The mathematical demography of the California Condor population. Amer. Nat. 105:437-453.
- Newton, I. and M. Marquiss. 1982. Fidelity to breeding area and mate fidelity in Sparrowhawks (Accipiter nisus). J. Anim. Ecol. 51:327-341.
- Nichols, J.D., G.L. Hensler and P.W. Sykes, Jr. 1980. Demography of the Everglade Kite: implications for population management. Ecol. Modelling 9:215-232.
- Postupalsky, S. 1974. Raptor reproductive success: some problems with methods, criteria and terminology. Raptor Res. Rept. 2: 21-31.
- Seber, G.A.F. 1965. The multi-sample single recapture census. Biometrika 49:330-349.
- Simberloff, D. 1987. The Spotted Owl fracas: mixing academic, applied, and political ecology. Ecology 68:766-772.
- Sisco, C. 1984. Winter ecology of radio-tagged Spotted Owls on Six Rivers National Forest, Humboldt Co., California. Unpubl. Tech. Rep., USDA - Forest Serv., Six Rivers National Forest, Eureka, CA. 140pp.
- Sokal, R.R. and F.J. Rohlf. 1981. Biometry. W.H. Freeman and Co., San Francisco. 859pp.
- Solis, D.M. 1983. Summer habitat ecology of Spotted Owls in northwestern California. M.S. Thesis, Humboldt State University, Arcata, CA. 169pp.
- Southern, H.N. and V.P.W. Lowe. 1968. The pattern of distribution of prey and predation in Tawny Owl territories. J. Anim. Ecol. 37:75-97.
- Tacha, T.C., W.D. Warde and K.P. Burnham. 1982. Use and interpretation of statistics in wildlife journals. Wildl. Soc. Bull. 10:355-362.

- Tanner, J.T. 1978. Guide to the study of animal populations. Univ. Tennessee Press, Knoxville. 186pp.
- U.S. Fish and Wildlife Service. 1982. The Northern Spotted Owl: a status review. Unpubl. Tech. Rep., U.S. Dept. Interior, Portland, OR. 29pp.
- Village, A. 1985. Turnover, age and sex ratios of Kestrels (Falco tinnunculus) in south Scotland. J. Zool. London (A) 206: 175-189.
- Woolfenden, G.E. and J.W. Fitzpatrick. 1984. The Florida Scrub Jay: demography of a cooperative-breeding bird. Princeton Univ. Press, Princeton, N.J. 406pp.
- Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall, Englewood, N.J. 718pp.

Appendix 1. Location and occupancy of 43 Northern Spotted Owl territories in the Willow Creek Study Area, northwest California, from 1985 through 1988. M = male; F = female; P = pair; U = owls not detected but territory inadequately surveyed; 0 = owls not detected, territory adequately surveyed, N = territory not surveyed. General legal description is for most recent nest or roost site.

Territory		General Legal	Year			
Name	Acronym	Description (T,R,1/4 Sec.)	85	86	87	88
Ammon Guard Station	AMMON	5N, 5E, SE 8	P	P	P	P
Barney Cr.	BARNY	5N, 5E, NE 30	P	P	P	P
Bee Tree Cr.	BEETR	5N, 5E, SW 21	P	P	P	P
Brush Mountain	BRUSH	6N,5E,NW 18	P	P	P	P
Burnt Ranch	BURNT	5N, 6E, SW 9	P	P	P	P
Burnt Ranch School	BURRS	5N, 6E, NW 10	M	M	0	0
Cedar Grove	CEDAR	5N, 5E, NE 23	P	P	P	P
China Cr.	CHINA	6N, 5E, NW 9	U	N	F	0
Deep Gulch	DEEPG	5N, 6E, NE 6	P	P	P	P
E Fk Madden Cr.	EFMCR	5N, 5E, NW 8	P	P	P	P
E Fk Willow Cr. (N)	EFWCN	6N, 4E, SW 14	P	P	M	P
E Fk Willow Cr. (C)	EFWCC	6N, 4E, NE 23	P	P	P	P
E Fk Willow Cr. (\$)	EFWCS	6N, 4E, NE 26	M	P	P	P
Fourmile Cr.	FOURM	6N, 5E, SW 18	0	0	M	0
Gaynor Peak	GAYNO	5N, 5E, SE 35	F	U	P	P
Gray Cr.	GRAYC	6N, 6E, SW 33	P	P	M	M
Gray Ranch	GRAYR	6N, 6E, SE 33	P	P	P	P
Grouse Mt. (E)	GROME	5N, 5E, SW 33	M	U	P	P
Hennessey Cr.	HENCR	5N, 6E, SW 4	P	P	P	P
Hennessey Ridge (W)	HENRW	6N,6E,SW 30	0	U	P	0
Hogback Ridge (E)	HOGRE	5N, 5E, SW 15	P	P	P	P
Horse Mt. Cr.	HORSE	5N, 4E, NW 2	0	0	0	P
Icebox Cr.	ICEBX	6N, 6E, NW 29	P	P	P	P
Madden Cr. (C)	MADCC	5N, 5E, NE 6	P	P	P	P
Mahala Cr.	MAHAL	6N, 5E, NE 2	M	P	0	M
McAlister Cr.	MCALI	4N,5E,NE 12	P	P	P	P
Mingo Cr. (C)	MINGC	5N, 5E, NW 35	0	0	0	P
Mingo Cr. (W)	MING0	5N, 5E, SE 34	P	P	P	P
Mosquito Cr. (N)	MOSCN	5N, 5E, SW 28	P	P	M	P
Mosquito Cr. (C)	MOSCC	4N, 5E, SE 5	P	P	P	P
Mosquito Cr. (S)	MOSCS	4N, 5E, SW 9	P	P	P	P
N Fk Madden Cr. (N)	NFMCN	6N, 4E, NE 24	M	M	P	P
N Fk Madden Cr. (C)	NFMCC	6N, 4E, SE 24	P	M	0	0
N Fk Madden Cr. (S)	NFMCS	6N, 5E, SE 24	P	P	P	P
Oak Knob (N)	OAKKN	6N, 5E, SW 28	M	U	P	P
Oak Knob (S)	OAKKS	5N, 5E, NE 9	P	P	P	P
Panther Ridge	PANTH	6N, 5E, NW 5	0	0	0	P
Pony Cr.	PONY	6N, 6E, SW 32	0	0	0	P
Sims Cr.	SIMSC	4N, 5E, SE 10	P	P	P	P
Spike Buck Cr.	SPIKE	5N, 5E, NW 32	P	P	P	0
Sugarloaf Mt. (N)	SUGRN	5N, 5E, NE 33	P	P	P	P
Sugarloaf Mt. (S)	SUGRS	5N, 5E, SE 33	P	P	P	P
SW Fk Madden Cr.	SWFMC	5N, 5E, NW 7	P	P	P	P